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Cleaner Shrimp Use a Rocking Dance to Advertise Cleaning Service to Clients

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Summary

Signals transmit information to receivers about sender attributes, increase the fitness of both parties, and are selected for in cooperative interactions between species to reduce conflict [1, 2]. Marine cleaning interactions are known for stereotyped behaviors [3–6] that likely serve as signals. For example, "dancing" and "tactile dancing" in cleaner fish may serve to advertise cleaning services to client fish [7] and manipulate client behavior [8], respectively. Cleaner shrimp clean fish [9], yet are cryptic in comparison to cleaner fish. Signals, therefore, are likely essential for cleaner shrimp to attract clients. Here, we show that the yellow-beaked cleaner shrimp [10] *Urocaridella* sp. c [11] uses a stereotypical side-to-side movement, or "rocking dance," while approaching potential client fish in the water column. This dance was followed by a cleaning interaction with the client 100% of the time. Hungry cleaner shrimp, which are more willing to clean than satiated ones [12], spent more time rocking and in closer proximity to clients *Cephalopholis cyanostigma* than satiated ones, and when given a choice, clients preferred hungry, rocking shrimp. The rocking dance therefore influenced client behavior and, thus, appears to function as a signal to advertise the presence of cleaner shrimp to potential clients.

Results and Discussion

Cleaner shrimp live in traditional sites, known as cleaning stations, that client fish visit to be cleaned [13]. Signals may therefore be essential for these cleaners to communicate to potential client fish that they are cleaners and whether they are willing to clean. The cleaner shrimp *Urocaridella* sp. c lives in groups in small caves and crevices on the reef and is not associated commensally with other animals. *Urocaridella* sp. c is mainly transparent, with scattered red and yellow spots on its body, two pairs of yellow chelate pereiopods, and a bright yellow line extending from the anterior end of its rostrum under the body to the telson, where it splits into two stripes continuing to the tips of the outer uropods. To determine whether *Urocaridella* sp. c advertise their cleaning services to client fish, we identified potential signal(s) in the wild and then tested in the laboratory whether these signal(s) attracted the client fish *Cephalopholis cyanostigma*. If signaling results in more cleaning for cleaner shrimp, and thus potentially increases their fitness, then signaling should increase as the cleaner's desire to clean increases. Becker and Grutter [12] showed that hunger level can affect a cleaner shrimp's desire to clean. They manipulated the hunger levels of cleaner shrimp and found that starved cleaner shrimp spent almost twice as much time cleaning client fish as satiated shrimp did. Therefore, we manipulated the cleaner shrimp's hunger level in the laboratory and exposed them to client fish to determine whether hunger level affected the potential signaling behavior of the cleaner shrimp. We then tested whether the behavior of the client fish *Cephalopholis cyanostigma* toward cleaner shrimp varied according to the potential advertising signal. The latter was manipulated by varying the hunger level of the cleaner shrimp.

In the wild, we found that when a potential client swam near a cleaning station, one to several cleaner shrimp performed a stereotypical, side-to-side movement or "rocking dance" while approaching the potential client in the water column. This dance was followed by a cleaning interaction 100% of the time. Cleaning stations had 1–25 cleaner shrimp, and a mean (±SEM) of 27.7 (± 14.4) clients were observed being cleaned per hour. *Urocaridella* sp. c has also been observed rocking for 45 client species, including the model client fish used here, *Cephalopholis cyanostigma* (J.H.A. Becker, unpublished data). When *Urocaridella* sp. c were not rocking or crawling on the surface of a client fish, they always remained still and attached to the wall of their shelter ("resting"). An anecdotal report also documents *Urocaridella* sp. c swimming into the water column and performing a rocking display dance while approaching fish [10]. Stereotyped behaviors have been described for other species of cleaner shrimp. For example, the cleaner shrimp *Urocaridella antonbruunii* (also incorrectly known as *Leandrites cyrtorhynchus* [11]) has been observed positioning itself in open water near its cleaning station [14]. Holzberg [14] noted that such posturing makes the shrimp conspicuous, suggesting this behavior may serve to attract fish. The cleaner shrimp *Stenopus hispidus* and *Periclimenes* spp. perform vigorous whipping of their antennae and lateral body swaying while standing in a conspicuous location when a client fish is nearby. As in cleaner fish, this behavior has been described as a "dance" in cleaner shrimp [5, 13, 15–17]. Dancing in cleaner fish is well known and may function to attract clients [3, 4, 7], although this has never been tested experimentally, or to avoid aggression [4, 7, 8, 18, 19]. Thus, there may be convergent evolution of cleaners' signaling, which facilitates their recognition by client fish [20].

In the laboratory, we examined the cleaner shrimp's behavior by exposing two shrimp to the same client behind glass. The starved cleaner engaged in a rocking dance 2× more frequently (mean ± SEM: 464.06 ± 38.28 per 70 min of observation) than did the satiated one (226.75 ± 46.85) (analysis of variance [ANOVA]: $F_{1,30}$ = 15.39, p = 0.0005). The same starved cleaner shrimp were observed 1.6× more often in the experimental-aquarium section nearest to the client than were the

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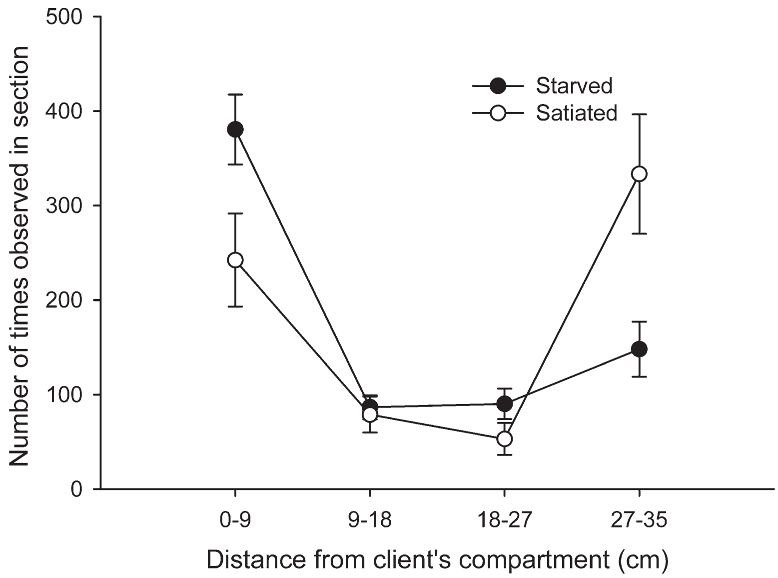

Figure 1. The Mean Number of Instantaneous Scans in Which Two Cleaner Shrimp *Urocaridella* sp. c Were Observed at Different Distances from the Client Fish (*Cephalopholis cyanostigma*) Compartment during 70 min of Observation over 110 min

n= 16. Shrimp location was recorded every 5 s. Error bars show the standard error.

satiated cleaner shrimp (ANOVA: $F_{1,30}$= 5.03, p = 0.03) (Figure 1). Satiated cleaners, in contrast, were observed more often in the section furthest from the client than were starved cleaners. Hunger increases a cleaner shrimp's desire to clean [12]. This implies that in the present study, the hungry cleaners were more willing to clean than were the satiated ones. Thus, the rocking dance and proximity to clients are likely a measure of a cleaner shrimp's desire to clean.

We examined the client's behavior toward cleaner shrimp by giving them a choice of two cleaner shrimp behind glass. Clients spent 11× more time (analyzed as $\log_{10}$ s) with the starved cleaner (mean ± SEM; 3.02 ± 0.16) than with the satiated one (1.98 ± 0.21; ANOVA: $F_{1,22}$ F = 15.88, p = 0.0006). The starved cleaners also rocked 8.3× more frequently (analyzed as arcsine [proportion of times rocking when the client entered the cleaner's area]) (mean ± SEM; 1.04 ± 0.13) than satiated ones (0.36 ± 0.13; ANOVA: $F_{1,22}$ F = 15.77, p = 0.0006). This result suggests that variation in the cleaners' behavior affected the client's choice of cleaner. Most likely, this behavior was rocking because no other potential signals were observed. This, combined with the observations in the wild, where cleaning was always preceded by a rocking dance, suggests that the rocking dance by the cleaner shrimp serves as a signal to attract client fish. Cleaner fish *Labroides dimidiatus* also engage in stereotyped dancing, assumed to also play a role in advertising [3, 4, 7], and appear to vary the intensity of the dance depending on the attractiveness of the client [4].

Signaling in *Urocaridella* sp. c probably involves a combination of movement, proximity, and color, all factors known to increase the conspicuousness of animals. Vision is highly sensitive to relative motion [21], and the eyes of some fish can detect moving objects more easily than stationary ones [22–24]. Thus, by using movement in the form of a rocking dance, cleaner shrimp may be more visible to clients. Reef fish are known to have poor resolving power [25]. Therefore, being in close proximity to a client while dancing may increase the likelihood that signals produced by the cleaner shrimp are visible to the client. Finally, the color yellow is a very conspicuous color when the background is blue [26]. Because the dominant color in *Urocardella* sp. c is yellow (J.H.A. Becker, unpublished data), its color is likely to stand out when the cleaner is away from the reef.

Advertising behavior has often been described for animals [27–30]; however, the term advertising is often interchangeable with display or signaling behavior. Here, we use the market definition that advertising is the placement of persuasive messages in time or space by individuals (or groups) who seek to inform and/or persuade members of a particular target market about their services [31]. On the basis of this definition, for a signal to be an advertisement, in a given area there must first be more than one individual using the signal to compete with nearby signalers for the attention of a receiver [32, 33]. The reefs surveyed had more than one cleaning station with *Urocaridella* sp. c, and many reefs had other cleaner shrimp species (e.g., *Periclimenes holthuisi*, *P. magnificus*, *Urocaridella* sp. a and b, *Lysmata amboinensis*, and *Stenopus hispidus*) and cleaner fish *Labroides dimidiatus* (J.H.A. Becker, unpublished data). Therefore, clients likely had several cleaners to choose from, suggesting that there is competition among cleaners for clients. Second, the signal should be costly to produce [32, 33]. The rocking dance is likely to be costly for cleaner shrimp to produce because it may attract the unwanted attention of potential predators as well as being energetically costly to produce. Third, if the receiver chooses to interact with a particular signaler, the resulting interaction should presumably increase the fitness of both the sender and the receiver [33]. Cleaner shrimp remove and eat ectoparasites from client fish [9], and this energy reward should increase the fitness of both the cleaner shrimp and the client. The relationship between cleaner shrimp and their clients satisfies the requirements that the rocking dance functions as an advertisement for cleaning services.

The use of advertising by *Urocaridella* sp. c satisfies one of the assumptions of biological markets. Biological market theory likens the interactions between animals to trade agreements involving the exchange of commodities and has been used to understand how cleaning mutualisms function [8, 12, 34–37]. In the cleaning mutualism, two different classes (the cleaner and the client) offer each other commodities (a cleaning service by the cleaner and food in the form of ectoparasites by the client) [34]. As in human markets, traders must advertise their commodities, making advertising one of the assumptions of a biological market [38]. Several other assumptions of biological markets [39] have previously been demonstrated for the *Urocaridella* sp. c-client fish system. First, *Urocaridella* sp. c and their clients also exchange such commodities [9]; second, partner choice by *Urocaridella* sp. c is based on the value of the commodity on offer (i.e., ectoparasite load); and third, supply and demand (i.e., ectoparasite load and cleaner-shrimp hunger levels) controls the commodity value [12]. The use of advertising, in addition to the other assumptions met, suggests that market theory can be used to better understand the interactions between cleaner shrimp and their clients.

Experimental Procedures

Observations of the cleaner shrimp *Urocaridella* sp. c and its client fish *Cephalopholis cyanostigma* were made at 16 cleaning stations between 7:00 a.m. and 5:00 p.m. on reefs around the Lizard Island Group, Australia, 23°27′ S, 151°55′ E between November 26 and December 8, 2001, March 23 and April 28, 2002, and January 5 and January 21, 2003. Divers swam around reefs and looked in caves and crevices for *Urocaridella* sp. c. Upon encountering cleaner shrimp, divers would stop approximately 2 m from the cleaners' cleaning station and observe the cleaners, usually for 15 min. The behaviors of both the cleaners and clients were recorded. During three separate observations, when no clients other than Apogonidae fish that appeared to be residents in the cleaning station were present, an individual *Urocaridella* sp. c swam from its cave toward the observing diver while rocking. On one of these occasions, the cleaner continued rocking back and forth while remaining within 1 m of its station for 5 min. These three observations were omitted from the analyses because it appeared that the cleaner was attempting to initiate a cleaning interaction with the diver. In the other observations, the diver did not appear to have any impact on cleaner-shrimp behavior. A total of 622 min of observation was made in the wild.

The laboratory experiments were conducted between January 5 and February 12, 2004 in a flow-through seawater system at Lizard Island Research Station. The client fish and cleaner shrimp were collected from reefs where field observations had been conducted previously. After capture by hook and line, ten clients were acclimatized in a 4 m diameter × 1.5 m holding tank for 2 to 10 days. An additional 18 fish were acclimatized in five smaller tubs (104.3 cm diameter × 40 cm) with three to four fish per tub. A shelter, consisting of a polyvinyl chloride (PVC) pipe (diameter 20 × 30 cm), was provided for each client. Clients were assumed to be acclimated to their new environment when they began feeding on chopped fish and prawn (usually between 1 and 2 days) that were provided to them daily. Cleaners were collected with hand nets and held for 2 to 10 days, prior to all trials, in four aquariums (50 × 50 × 70 cm) with 14–15 individuals per aquarium. Three shelters, consisting of PVC pipe (diameter 7 × 15 cm), per aquarium were provided for the cleaners.

Cleaner-Shrimp Behavior

On the basis of the field observations that revealed that cleaner shrimp engaged in a rocking dance while approaching clients (see Results and Discussion), this behavior was selected as a potential signal that these cleaners might use to attract clients. Two cleaners, one with a high willingness and one with a low willingness to clean, were exposed to a client to determine whether the rocking dance and the proximity of cleaners to clients varied with the cleaners' willingness to clean. The two cleaners were placed in a compartmentalized aquarium with a client fish behind glass, and the cleaners' behavior and proximity to the client were recorded. Because starved cleaners are more willing to clean clients than satiated ones [12], willingness to clean was varied by manipulating the hunger level of the cleaner. For each trial, one cleaner was fed to satiation with a piece of prawn (0.5 cm^3) 3 times a day for 3 days, and the other was not fed for 3 days prior to the experiment. Cleaners were kept individually in fine mesh (0.01 × 0.01 cm) chambers (10 × 10 × 15 cm) prior to the experiment to prevent them from obtaining fine food particles or zooplankton from the seawater. The two cleaners were exposed to a client in an experimental aquarium (37 × 37 × 91 cm). The experimental aquarium was divided into three main compartments across the front 91 cm plane with clear Perspex sheets. At either end of the aquarium was a compartment (36 × 37 × 37 cm) for each cleaner, and the center compartment (19 × 37 × 37 cm) held the client. A shelter, consisting of PVC pipe (diameter 10 × 20 cm), was provided for the client. The width of the client's compartment enabled the client to enter and exit the shelter, but not swim toward or away from either cleaner. This was done to minimize the client's influence on the behavior of the cleaner. Any movements by the client were recorded. However, client movements were infrequent (zero to two movements per trial; movements involved turning the body to face toward or away from the front of the aquarium) because *C. cyanostigma* is a highly sedentary species [40]. Therefore, the client's movements were not considered further. The cleaner's compartment was divided into four 9 cm sections across the 36 cm front plane with black permanent marker pen on the outside of the aquarium. The water level was kept constant at a depth of 34 cm. The client was placed into the central compartment 24 hr before the trial to acclimate to its new environment. The trial began when both cleaners were released into their respective compartments at the same time. The cleaner and client were observed for seven 10 min blocks over a 100 min period. Time intervals began at 0, 10, 20, 30, 40, 70, and 90 min, respectively. Every 5 s, the section of the compartment the cleaner was in and the cleaner's behavior were recorded. Cleaner behavior was categorized as either rocking (i.e., swimming about its compartment while occasionally rocking side to side without contacting any surface) or resting (i.e., on a surface and not moving). Different shrimp and clients were used in all the trials (n = 16). The number of instantaneous scans in which the cleaners were observed rocking per 10 min time interval and the number of times each cleaner was observed in the nearest section to the client (0–9 cm) were analyzed separately. The factor "time interval" was initially used in separate repeated measures analyses of variance (ANOVA; Statistica Version 6). However, because there was no interaction between time interval and hunger level on the time cleaners spent rocking ($F_{6,180} = 0.63$, $p = 0.70$) or on the time cleaners spent rocking in the section nearest to the client ($F_{6,180} = 1.88$, $p = 0.09$), the repeated measure, time interval, was dropped from both models, and all the data were pooled across time intervals and analyzed with one-way ANOVAs (JMP In Version 4).

Client-Fish Response to Cleaner Shrimp

A client was placed in a tub with one cleaner with a high willingness and one with a low willingness to clean, and the time the client spent in close proximity to each cleaner was recorded to determine whether cleaner-shrimp behavior attracts client fish. Cleaner hunger level (willingness to clean) was manipulated as above. A client was placed in a tub (104.3 cm diameter × 40 cm), and the two cleaners were each placed in an aquarium (17 deep × 25 wide × 6 high cm) at opposite sides of the tub and touching the tub wall. The time that the anterior part of the client's head was within a radius of 39 cm from the aquarium wall behind the cleaner's aquarium (the area surrounding the aquarium is referred to as the cleaner's area henceforth) was recorded. This distance allowed for a relatively large neutral area between the two cleaners. We assumed that time spent within the cleaner's area represented interest in the cleaner by the client. Each trial began after the client fish entered both of the cleaners' areas and then returned to the neutral area to ensure that the client was aware of both cleaners.

For the observers to approach near enough to the cleaner shrimp to observe them for the entire trial could potentially have influenced the behavior of the client fish (although we did not observe any obvious effect of observers on client behavior). Therefore, the behavior (resting or rocking) of each cleaner was only recorded as a proportion of the number of times the client entered that particular cleaner's area. The total proportions were arcsine transformed to satisfy the assumptions of the analysis. The side of tub (left or right) that the aquarium was positioned in was alternated for each trial in a random but balanced way to control for an effect of tub side on client preference. The total time the client spent in each cleaner's area was recorded over 2 hr, and the data were analyzed with one-way ANOVAs (JMP In Version 4). Different cleaners and clients were used in all the trials (n = 12).

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References

1. Tinbergen, N. (1964). The evolution of signalling devices. In Social Behaviour and Organization among Vertebrates, W. Etkin, ed. (Chicago and London: University of Chicago Press), pp. 206–230.
2. Dawkins, R., and Krebs, J.R. (1978). Animal signals: Information or manipulation. In Behavioural Ecology: An Evolutionary Approach, J.R. Krebs and N.B. Davies, eds. (Oxford: Blackwell Scientific Publications), pp. 282–309.
3. Wickler, W. (1968). Mimicry in Plants and Animals (London: Weidenfeld and Nicolson).
4. Potts, G.W. (1973). The ethology of *Labroides dimidiatus* (Cuv. & Val.) (Labridae, Pisces) on aldabra. Anim. Behav. *21*, 250–291.
5. Limbaugh, C. (1961). Cleaning symbiosis. Sci. Am. *205*, 42–49.
6. Feder, H.M. (1966). Cleaning symbiosis in the marine environment. In Symbiosis, S.M. Henry, ed. (New York: Academic Press), pp. 327–380.
7. Youngbluth, M.J. (1968). Aspects of the ecology and ethology of the cleaning fish, *Labroides phthirophagus* Randall. Z. Tierpsychol. *25*, 915–932.
8. Grutter, A.S. (2004). Cleaner fish use tactile dancing behavior as a preconflict management strategy. Curr. Biol. *14*, 1080–1083.
9. Becker, J.H.A., and Grutter, A.S. (2004). Cleaner shrimp do clean! Coral Reefs *23*, 515–520.
10. Coleman, N. (1993). Australian Fish Behaviour (Rochedale, South Australia: Underwater Geographic Pty Ltd).
11. Debelius, H. (1999). Crustacea Guide of the World (Frankfurt: Ikan).
12. Becker, J.H.A., and Grutter, A.S. (2005). Client-fish ectoparasite loads and cleaner-shrimp *Urocaridella* sp. c hunger levels affect cleaning behaviour. Anim. Behav., in press.
13. Limbaugh, C., Pederson, H., and Chace, F.A., Jr. (1961). Shrimps that clean fishes. Bulletin of Marine Science of the Gulf and Caribbean. *11*, 237–257.
14. Holzberg, S. (1971). Beobachtung einer Putzsymbiose zwischen der Garnele *Leandrites cyrtorhynchus* und Riffbarschen. Helgolander Meeresuntersuchungen. *22*, 362–365.
15. Sargent, R.C., and Wagenbach, G.E. (1975). Cleaning behavior of the shrimp, *Periclimenes anthophilus* Holthius and Eibl-Eibesfeldt (Crustacea: Decapoda: Natantia). Bull. Mar. Sci. *25*, 466–472.
16. Dreyer, K.B. (1994). Cleaning symbiosis between shrimp (Hippolytidae) and moray eels (Muraenidae): Primitive or advanced? Proceedings: The 26th Meeting of the Association of Marine Laboratories of the Caribbean. June 11–16, 1994. The Bahamian Field Station Ltd. San Salvador, Bahamas, 1–16a.
17. Kulbicki, M., and Arnal, C. (1999). Cleaning of fish ectoparasites by a Palaemonidae shrimp on soft bottoms in New Caledonia. Cybium. *23*, 101–104.
18. Losey, G.S. (1971). Communication between fishes in cleaning symbiosis. In Aspects of the Biology of Symbiosis, T.C. Cheng, ed. (Baltimore: University Park Press), pp. 45–76.
19. Sazima, I., Moura, R.L., and Gasparini, J.L. (1998). The wrasse *Halichoeres cyanocephalus* (Labridae) as a specialized cleaner fish. Bull. Mar. Sci. *63*, 605–610.
20. Stummer, L.E., Weller, J.A., Johnson, M.L., and Côté, I.M. (2004). Size and stripes: How fish clients recognize cleaners. Anim. Behav. *68*, 145–150.
21. Nakayama, K. (1985). Biological image notion processing: A review. Vision Res. *25*, 625–660.
22. Schaerer, S., and Neumeyer, C. (1996). Motion detection in goldfish investigated with the optomotor response is "Color Blind". Vision Res. *36*, 4025–4034.
23. Engstrom, K. (1963). Cone types and cone arrangements in teleost retinae. Acta zoologica. *44*, 179–243.
24. Boehlert, G.W. (1978). Intraspecific evidence for the function of single and double cones in the teleost retina. Science *202*, 309–311.
25. Marshall, N.J. (2000). Communication and camouflage with the same "bright" colours in reef fish. Philos. Trans. R. Soc. Lond. B Biol. Sci. *355*, 1243–1248.
26. Marshall, N.J., Jennings, K., McFarland, W.N., Loew, E.R., and Losey, G.S. (2003). Visual biology of Hawaiian coral reef fish. III. Environmental light and an integrated approach to the ecology of reef fish vision. Copeia *2003*, 467–480.
27. Beatty, C.D., Beirinckx, K., and Sherratt, T.N. (2004). The evolution of müllerian mimicry in multispecies communities. Nature. *431*, 63–67.
28. Seeley, T.D., and Visscher, P.K. (2003). Choosing a home: How the scouts in a honey bee swarm perceive the completion of their group decision making. Behav. Ecol. Sociobiol. *54*, 511–520.
29. Alonso-Alvarez, C., Doutrelant, C., and Sorci, G. (2004). Ultraviolet reflectance affects male-male interactions in the blue tit (*Parus caeruleus ultramarinus*). Behav. Ecol. *15*, 805–809.
30. Losey, G.S. (1987). Cleaning Symbiosis. Symbiosis *4*, 229–258.
31. Bennett, P.D. (1995). Dictionary of Marketing Terms (Lincolnwood, Illinois: NTC Business Books).
32. Maynard-Smith, J. (1991). Theories of Sexual Selection. Trends Ecol. Evol. *6*, 146–151.
33. Johnstone, R.A. (2000). Conflicts of interest in signal evolution. In Signalling and Signal Design in Animal Communication, Y. Espmark, T. Amundsen, and G. Rosenqvist, eds. (Trondheim, Norway: Tapir Academic Press), pp. 465–485.
34. Bshary, R. (2001). The cleaner fish market. In Economics in Nature: Social Dilemmas, Mate Choice and Biological Markets, R. Noë, J.A.R.A.M. Van Hooff, and P. Hammerstein, eds. (Cambridge: Cambridge University Press), pp. 146–172.
35. Bshary, R., and Wurth, M. (2001). Cleaner fish Labroides dimidiatus manipulate client reef fish by providing tactile stimulation. Proc. R. Soc. Lond. B. Biol. Sci. *268*, 1495–1501.

36. Bshary, R., and Schaffer, D. (2002). Choosy reef fish select cleaner fish that provide high-quality service. Anim. Behav. *53*, 557–564.
37. Bshary, R., and Grutter, A.S. (2002). Parasite distribution on client reef fish determines cleaner fish foraging patterns. Mar. Ecol. Prog. Ser. *235*, 217–222.
38. Noë, R. (2001). Biological markets: Partner choice as the driving force behind the evolution of mutualisms. In Economics in Nature, R. Noë, J.A.R.A.M. Van Hooff, and P. Hammerstein, eds. (Cambridge: Cambridge University Press), pp. 93–118.
39. Noë, R., and Hammerstein, P. (1995). Biological markets. Trends Ecol. Evol. *10*, 336–339.
40. Stewart, B.D., and Jones, G.P. (2001). Associations between the abundance of piscivorous fish and their prey on coral reefs: Implications for prey-fish mortality. Mar. Biol. *138*, 383–397.